DESTRUCTION OF MOSSES BY LICHENS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 287

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(WITH PLATE XIII)

The deep-rooted conception of lichens as typical examples of symbiosis has induced workers along ecological lines to overlook the occurrence in xerarch successions of early stages which are dominated by the parasitism of lichens on mosses. This preliminary paper is intended to describe certain cases of lichen parasitism, and to emphasize the accuracy of FINK'S definition of lichens: "A lichen is a fungus which lives during all or part of its life in parasitic relation with an algal host, and also sustains a relation with an organic or inorganic substratum."

The writer's attention was first called to this situation when trying to separate some *Cladonia* lichen material from a moss colony in which it was growing. The intimacy of the mixture suggested that the lichen might be to some extent parasitic on the moss. Such phenomena seem to have been noticed previously by BONNIER,[1] who shows that spores of lichens are known to germinate on moss protonemas and eventually to attack and kill them. He suggests the occurrence of such parasitism in nature on a large scale.

Moss-lichen colonies were chosen for study, in which both elements were intimately mixed, illustrating cases of dominance on the part of one or the other. It was often impossible to determine the exact species or even genus of the mosses concerned, because of the poor condition of the vegetative body and lack of reproductive organs. Mosses hampered by invading lichens seldom produce spores. Representative lichen-moss mixtures consisting of species

[1] BONNIER, GASTON, Germination des spores des Lichens sur les protonemas des Mousses et sur des Algues differents des gonidies du Lichen. Compt. Rend. Soc. Biol. Paris. 40:541–543. 1888.

———, Germination des Lichens sur les protonemas des Mousses. Rev. Gen. Bot. 1:165–169. *pl. 8.* 1899.

of *Dicranum*, *Bryum*, *Grimmia*, or *Fissidens* with *Cladonia*, *Physcia*, or *Amphiloma* have been collected. The following species determinations of mosses based on vegetative characters may be taken as probable: *Dicranum scoparium*, *Bryum caespiticium*, *B. argenteum*, *Grimmia apocarpa*, *G. pennsylvanica*, and *Fissidens adiantoides*. Especially important among the lichens concerned are *Cladonia cristatella*, *C. baccillaris*, *C. pyxidata*, *Physcia stellaris*, *P. obscura*, and *Amphiloma lanuginosum*.

All previous observations along this line are based on cultures and the examination of teased materials. The method employed consisted of imbedding and sectioning moss-lichen colonies, the resultant serial sections giving a veritable moving picture of the conditions in the colonies. The striking destruction of moss tissues is evident from sections 10 μ or more in thickness, but to judge the extent and nature of the haustorial action it is necessary to have sections 3 μ or less in thickness. Many kinds of fixatives were used to show to the best advantage the various tissues concerned; no one fixative gave the most satisfactory fixation for all. The fungus elements of the lichen fix well in chromoacetic; the algal elements in hot bichloride of mercury. The location of the nucleus in the algal cells, and the condition of plastids in the moss show well in aceto-formalin. The cell wall structures of all the tissues showed best in aceto-formalin. Very weak Flemming's solution gave excellent results in the young tissues of the moss. The three tissues, moss, fungus, and alga, can be sharply differentiated by a carefully balanced Flemming's triple stain. For wall studies nothing proved better than a contrasting safranin-analin-blue stain. With this stain the cell wall changes and the haustorial action may be clearly demonstrated. Slides so stained were easily photographed by suitable combinations of yellow and green filters. In addition to the section studies, a long series of cultures was run with *Amphiloma* and other lichen genera to see how readily and under what conditions they would attack a moss host.

The destructive action of lichens on moss may be seen from figs. 1 and 2. These were from 10 μ sections of intimate mixtures of *Cladonia* lichens with *Dicranum*, *Grimmia*, and other mosses,

in which the moss appears plastered over by the lichens. The apical development of the moss has been stopped. The lichen hyphae could be traced through the old moss tissue where they forced their way intercellularly.

A very constant feature of the lichen growth on mosses is the clinging of the lichen hyphae to the thickened walls of the moss. This seems to be of great significance in the eventual destruction of the moss colony. It is not the meristematic tissue that seems particularly desirable to the lichen fungus, but the thickenings of the moss walls. The case seems homologous with the destruction of wood by a polyporous fungus, where the lignified part of the wood is especially attacked, and the cellulose walls are left almost untouched. In the mosses the young walls are pure cellulose; the thickenings are of pectin. Thin sections of all the moss-lichen colonies studied showed the hyphae imbedded in the pectin. There is no evidence that the hyphae have been covered over by the forming pectin layers, but it seems obvious that the hyphae have taken their position by dissolving out the pectin. The figures of *Amphiloma* on *Grimmia* show a case of this, but *Amphiloma* is more destructive than most lichens, and in places has completely destroyed the moss. When sharply stained in safranin and analine blue, the pectinized part of the walls stains a strong red, so that penetration of the bluish stained hyphae may be plainly followed. In some colonies, even when the lichens appear to be literally plastered over the mosses, the lichen hyphae were found to be confined to the pectinized regions, and the cellulose walls to be intact; then the lichens are exerting a smothering effect carried on through a saprophytic rather than a parasitic action.

Lichen fungi sometimes become truly parasitic on their moss hosts. This is especially true of *Amphiloma*, which is shown in fig. 6. Here the lichen is an intracellular parasite. *Amphiloma* haustoria soon break down the plastids, even in old moss tissues. *Amphiloma* seldom attacks the meristematic tissues. Under some conditions *Physcia obscura* may send hyphae of non-rhizoidal nature into the meristematic moss tissues. *Physcia* also may so incorporate moss into its thallus, that the epidermis of the lichen

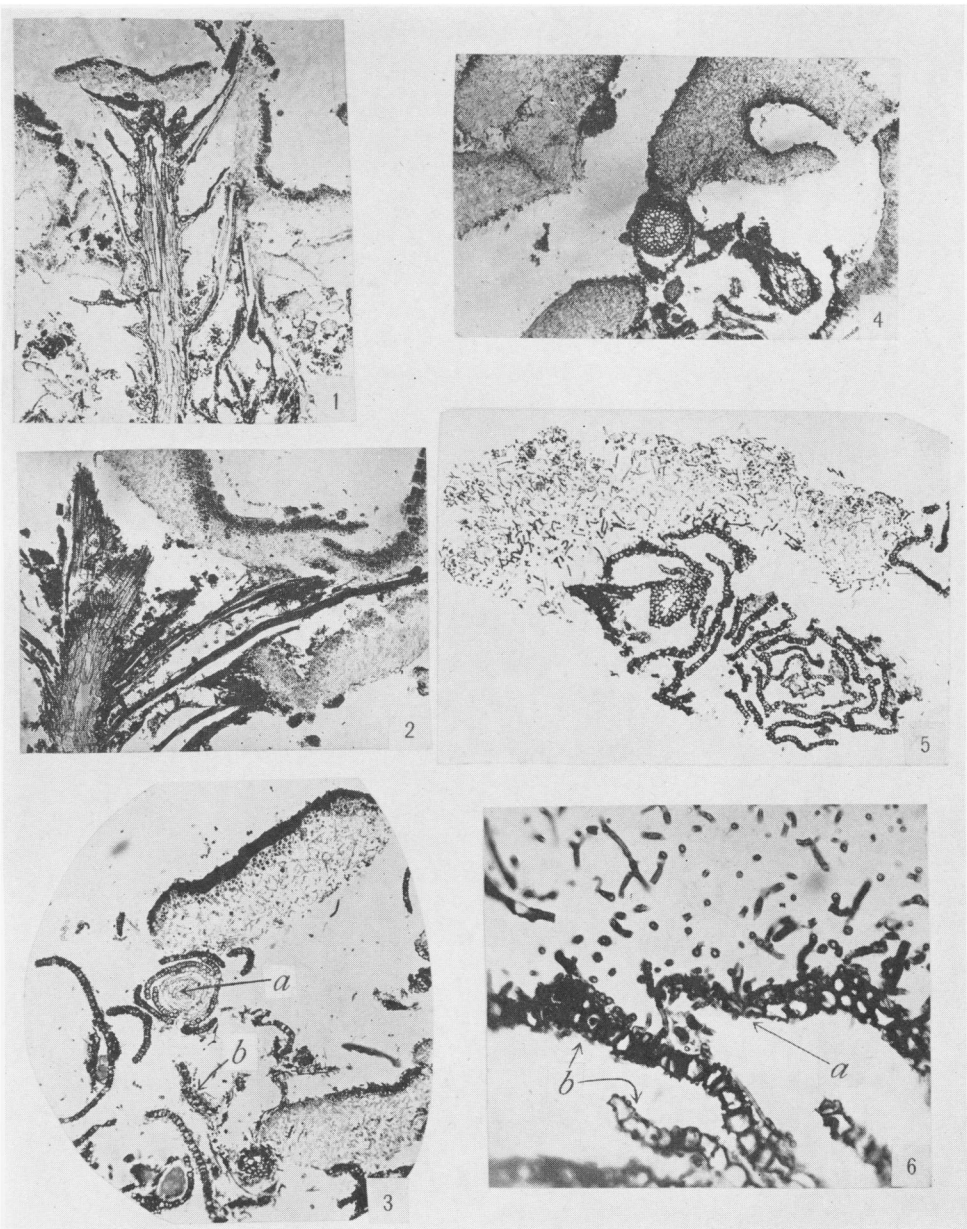
develops on the lower side of the moss leaf and the rest of the lichen on the other side, the moss becoming a veritable layer of the lichen. In such cases the moss leaf is eventually destroyed.

The great opportunity for the parasitizing of mosses by lichens, as they grow together in nature, cannot be over emphasized. For the most part the lichens develop on the leaves of the moss. Moss colonies in which apparently no lichens are present, when sectioned or teased out almost invariably show tiny young lichens developing in their leaves. Hundreds of lichens have been seen developing from soredial masses, but very few from spores, hence it is concluded that moss inhabiting lichens depend on soredia rather than on spores for reproduction. BONNIER'S observations on the ability of lichens to germinate on, and eventually to kill moss protonema, have already been mentioned. Since the protonemal stage is a transient one, it probably does not take place in nature to any great extent. The germination of lichens on moss leaves is the rule, so far as cases where lichens eventually plaster themselves over the mosses are concerned. The young lichen hyphae become attached from their first formation. The environmental factors control the future appearance of the colonies. From cultures and field observations it is concluded that water is the dominating factor of the control. Almost any moss colony, apparently free from lichens, when grown in semimoist conditions, but occasionally allowed to dry out, in a few weeks will produce young lichens visible to the naked eye.

If these observations are borne in mind, it is easy to see why so often the ideal lichen-moss-fern sequence is not carried out, since the sequence is broken up by lichen stages in which the lichens are more or less parasitic on the moss. If the rock surface is rough enough, visible life may be initiated by moss, and a lichen stage come in secondly. In any event a well established moss stage may be crowded out by a more or less parasitic lichen mass, which gives a secondary lichen stage succeeding the moss.

Summary

Lichens are able to destroy moss colonies. The destruction is partly due to true parasitism and partly to smothering.



McWHORTER on MOSSES AND LICHENS

The development of lichens in moss colonies makes possible the coming in of a lichen stage after the moss associations.

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EXPLANATION OF PLATE XIII

The illustrations are all photomicrographs selected from a much larger number showing similar conditions.

FIG. 1.—*Cladonia pyxidata* on moss, probably *Dicranum;* vertical section through colony showing moss plant with leaves cut to pieces and apical growth stopped by action of lichen.

FIG. 2.—*Cladonia pyxidata* on an unrecognizable moss; organization of moss leaves destroyed by action of lichen; lichen hyphae penetrated intercellularly through moss tissues.

FIG. 3.—Section of a moss-lichen mixture cut parallel to surface of colony, showing lichen (*Cladonia*) hyphae penetrated into cells of apical region of moss (*Grimmia*); hyphae indicated by arrow *a* could be traced through serial sections to lichen mass just above; *b*, moss leaf strongly attacked by hyphae.

FIG. 4.—Section from lower part of colony cut parallel to surface, showing lichen hyphae tending to fuse with pectinized walls of moss tissues.

FIG. 5.—Section through a *Amphiloma-Grimmia* mixture; *Amphiloma* has organized on moss leaf; this lichen probably destroys more moss than any other.

FIG. 6.—Portion of fig. 5 more highly magnified, showing: *a*, how lichen may completely destroy moss cells; *b*, how hyphae dissolve pectinized layer of cell walls of moss.